Two Neogene vesicomyid species (Bivalvia) from Japan and their biogeographic implications

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ABSTRACT

A new species of the bivalve family Vesicomyidae, *Calyptogena veneriformis*, is described from the Pliocene part of the Kurokura Formation in Niigata Prefecture, Japan. This species belongs to the Plio-Pleistocene Omma-Manganji fauna on the coast of the Japan Sea. We document previously unknown characters of the shell interior of "*Vesicomya*" *kawadai* (Aoki) from lower to middle Miocene deposits in Honshu, Japan, showing that the species belongs to the genus *Pliocardia*. The genus *Pliocardia* might have a longer geologic history than previously appreciated. When the currently known distribution of *Pliocardia* is taken at face value, the genus might have colonized the Atlantic Ocean only very recently, perhaps as late as the Pliocene, despite its long geologic history.

Additional keywords: Pliocardia, Vesicomya, Calyptogena, Plio-Pleistocene

INTRODUCTION

The Vesicomyidae is one of the six bivalve families living in symbiosis with chemoautotrophic bacteria, with a geologic history ranging back to the middle Eocene (Taylor and Glover, 2010; Kiel, 2010). Due to the limited number of shell characters and the high morphologic plasticity among the vesicomyids, Japanese malacologists often subdivided the family into two genera, *Calyptogena* Dall, 1891 for large elongate shells, and *Vesicomya* Dall, 1886 for small subcircular or veneriform shells (e.g. Sasaki et al., 2005). Recently, we have examined fossil representatives of large, elongate vesicomyids in the northern Pacific region (Amano and Kiel, 2007, 2010, 2011; Kiel and Amano, 2010) and distinguished four genera: *Calyptogena*, *Archivesica* Dall, 1908, *Adulomya* Kuroda, 1931, and *Hubertschenckia* Takeda, 1953.

The genus *Calyptogena* is composed of ten or more Recent species (Krylova and Sahling, 2006, 2010). Among them, only one species, *Calyptogena pacifica* Dall, 1891, has fossil representatives, ranging from the upper Miocene to the middle Pleistocene in the Japan Sea Borderland (Kanno et al., 1989; Amano, 2003; Amano and Kanno, 2005; Amano and Jenkins, 2011). We have now recovered one new species of *Calyptogena* from the Japan Sea borderland, from the lower Pliocene part of the Kurokura Formation in Niigata Prefecture.

Among the small vesicomyids ("*Vesicomya*"of Japanese malacologists), Cosel and Salas (2001) recognized several genera, namely *Vesicomya*, *Isorropodon* Sturany, 1896, *Waisiuconcha* Beets, 1942, and *Callogonia* Dall, 1889. In addition, Krylova and Janssen (2006) and Krylova and Sahling (2010) redefined the small vesicomyid genus *Pliocardia* Woodring, 1925, and included two Japanese species, *Vesicomya crenulomarginata* Okutani, Kojima, and Iwasaki, 2002 and *V. kuroshimana* Okutani, Fujikura and Kojima, 2000. According to these taxonomic revisions, the genus *Vesicomya* is now confined to very small species (3–13 mm long) having subcircular shells and thin cardinal teeth that are arranged roughly in a linear fashion. Three fossil species were reported as "*Vesicomya*" from Cretaceous and Neogene deposits in Japan: *Vesicomya kawadai* (Aoki, 1954), *V. inflata* Kanie and Nishida, 2000, and *V. ellipsoidea* Kanie and Kuramochi, 2001. Among them, Amano et al. (2008) showed that *V. inflata* from Cretaceous deposits in Hokkaido is a lucinid, not a vesicomyid, and established the new genus *Ezolucina* for this species. "*Vesicomya*" *ellipsoidea* has a large and elongate shell (up to 188.6 mm long) and two cardinal teeth in right valve and does therefore belong to *Archivesica* or *Adulomya* rather than *Vesicomya sensu stricto* (Amano and Kiel, 2011). The generic status of *Vesicomya kawadai* has so far remained uncertain.

The scope of the present contribution is (1) to describe and name the new species of *Calyptogena*, (2) to clarify the generic status of "*Vesicomya*" *kawadai* based on newly collected material, and (3) to discuss the biogeographic significance of these species.

MATERIALS AND METHODS

Several small vesicomyid specimens were recovered from calcareous concretions within the mudstone of the lower Pliocene part of the Kurokura Formation at Sugawa in Joetsu City, Niigata Prefecture (Figure 1, Loc. 1), and they occur in association with *Calyptogena pacifica* Dall, 1891 and the thyasirid bivalve *Conchocele bisecta* (Conrad, 1849). These specimens are described as *Calyptogena veneriformis* herein.

The specimens of "*Vesicomya*" *kawadai* examined herein are from the type locality of this species, in the lower Miocene Honya Formation at Donosaku in Iwaki City, Fukushima Prefecture (Figure 1, Loc. 2). The specimens were found in a large calcareous concretion where they co-occur with *Adulomya chitanii* Kanehara, 1937 and *Conchocele bisecta*. Some specimens of "*Vesicomya*" *kawadai* from the Honya Formation in the Ishimoriyama area of Iwaki City, Fukushima Prefecture (Figure 1, Loc. 3) were examined. These specimens were collected by the late Prof. Katsumi Hirayama of Rikkyo University, and the exact locality and the associated fauna are unknown. In addition, two specimens of "*Vesicomya*" *kawadai* were collected on the Rekifune River (Figure 1, Loc. 4), about 400 m downstream from the fossil whale-fall site described by Amano et al. (2007), in eastern Hokkaido. The specimens were collected from carbonaceous mudstones of the middle Miocene Nupinai Formation, which most likely represent an ancient cold-seep site, inferred from the associated species *Adulomya chitanii*, *Conchocele bisecta,* and *Portlandia* sp.

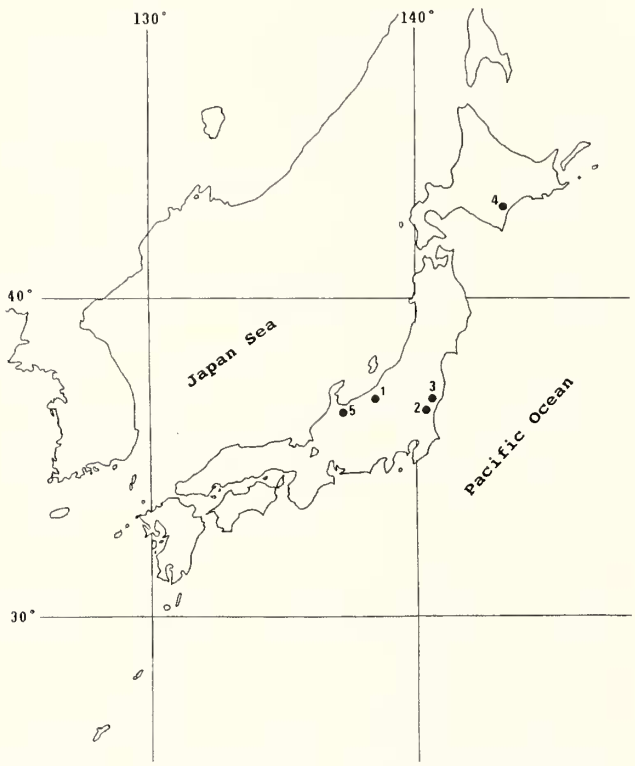


Figure 1. Localities of the fossil vesicomyids described herein. 1: Sugawa in Joetsu City, Niigata Pref. (lower Pliocene). 2: Donosaku in Iwaki City, Fukushima Pref. (lower Miocene); 3: Ishimoriyama area of Iwaki City, Fukushima Pref. (lower Miocene). 4: Rekifune River, Hokkaido (middle Miocene). 5: Shimo-sasahara, Toyama Prefecture (uppermost lower to lowermost middle Miocene). *Calyptogena veneriformis* was collected from Loc. 1. *Pliocardia kawadai* was recovered from Locs. 2–5.

We also reexamined the specimens of "*Vesicomya*" *kawadai* described by Amano et al. (2001) from the uppermost lower to lowermost middle Miocene Higashibessho Formation at Shimo-sasahara in Toyama Prefecture (Figure 1, Loc. 5). All specimens are deposited in the Joetsu University of Education (JUE).

SYSTEMATICS

Family Vesicomyidae Dall and Simpson, 1901
Subfamily Pliocardiinae Woodring, 1925

Genus *Pliocardia* Woodring, 1925

Type Species: *Anomalocardia bowdeniana* Dall, 1903 from the upper Pliocene Bowden Formation in Jamaica; by original designation.

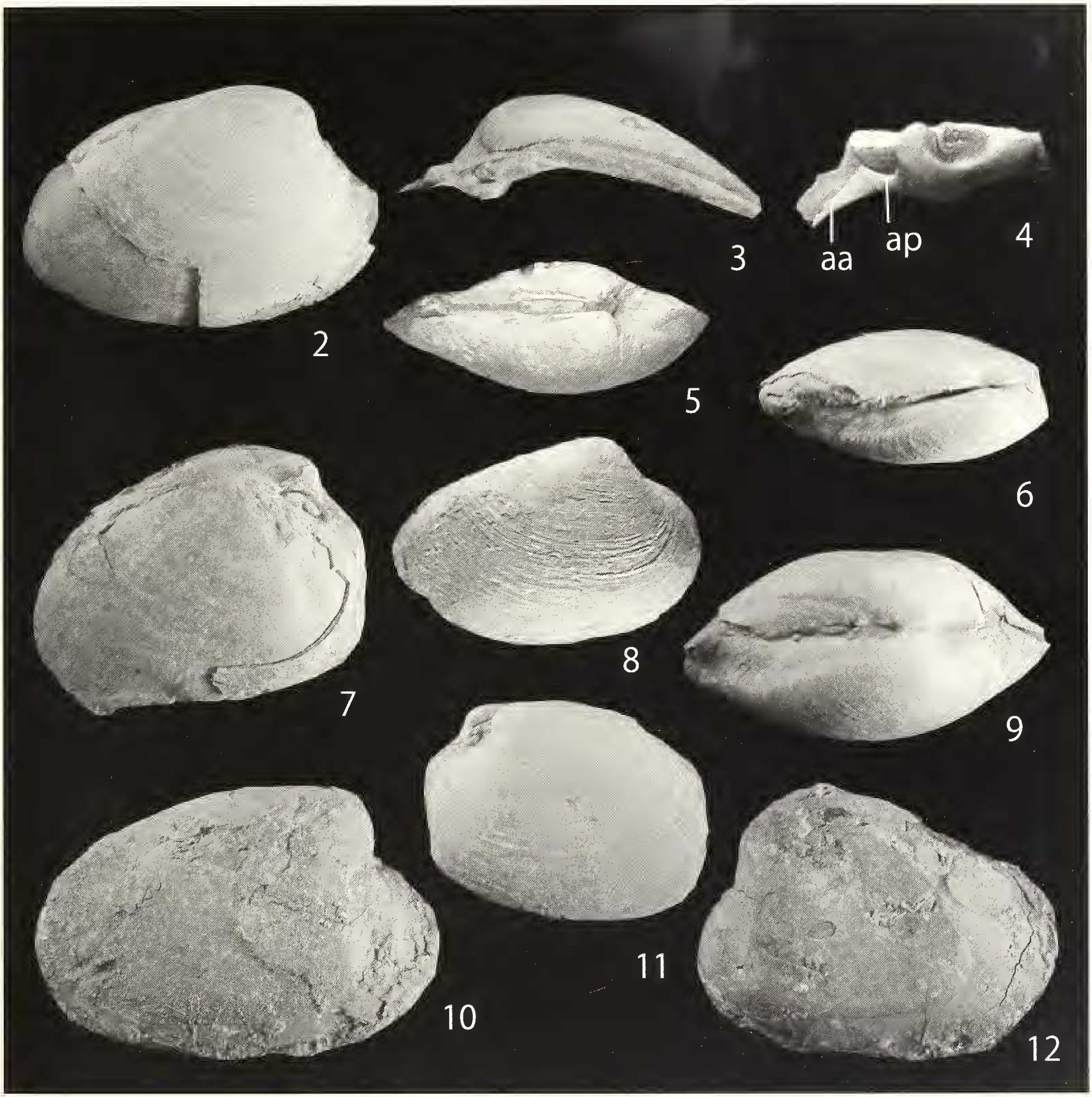
Remarks: According to the redefinition by Krylova and Janssen (2006), this genus is characterized by its small- to medium-sized elliptical shells having a shallow radial depression from beak to postero-ventral margin, a deep lunular incision, a shallow pallial sinus and a stout ventral tooth (1) overlying the subumbonal cardinal teeth (3a, 3b) in the right valve.

Pliocardia kawadai (Aoki, 1954)
(Figures 2–4, 6–7, 9–12)

Lamelliconcha kawadai Aoki, 1954: 36–37, pl.2, figs.1, 10, 12–15, 22.
Vesicomya kawadai (Aoki).—Kamada, 1962: 88–89, pl.8, figs. 2a–b; Amano et al., 2001: 192, figs. 3–5, 8–11; Amano et al., 2007: figs. 3D, E, G, J.

Description: Shell thin, medium sized (up to 40.7 mm long), ovate, with radial depression extending from beak to postero-ventral corner, with distinct, shallow lunular incision. Pallial sinus shallow and v-shaped, situated just before radial inner ridge extending from beak to posterior corner. On hinge of right valve, ventral tooth (1) thin to moderately thick, overlain by arched subumbonal teeth (3a, 3b); cardinal tooth 3b bifid in some specimens. Left valve hinge with thin cardinal tooth 2a and stout cardinal tooth 2b, connected with a thin tooth 4b. Anterior adductor muscle scar ovate with rather straight and sharp posterior margin; anterior pedal retractor scar with semi-circular shape, deeply impressed with rough striations subparallel to shell margin, located between hinge plate and anterior adductor muscle scar, from which it is separated by a sharp step. Posterior adductor muscle scar ovate or circular and deeply depressed.

Material Examined: Twenty-seven specimens: JUE nos. 15895, 15896, 15897.



Figures 2–12. *Pliocardia* species. **2–4, 6–7, 9–12.** *Pliocardia kawadai* (Aoki). **2, 3.** Right valve surface and hinge. Length 40.7 mm, hinge length 22.8 mm, JUE no. 15895-2; Loc. 3. **4.** Anterior pedal retractor scar. Illustrated hinge length 12.7 mm; aa, anterior adductor scar; ap, anterior pedal retractor scar; JUE no.15697; Loc. 5. **6, 11.** Right valve hinge and weak lunule incisa. Length 24.7 mm, JUE no. 15897-1; Loc. 4. **7.** Inner surface of right valve and left valve hinge. Length 32.6mm, JUE no. 15895-3, Loc. 3. **9.** Escutcheon and lunule incisa. Length 35.4 mm, JUE no. 15895-1; Loc. 3. **10.** Right valve. Length 40.0 mm, JUE no. 15896-1; Loc. 2. **12.** Inner surface of left valve. Length 35.4 mm, JUE no. 15896-2; Loc. 2. **5, 8.** *Pliocardia* sp. from an Oligocene seep carbonate in the Lincoln Creek Formation in Washington State, USA (LACMIP loc. 17447B, see Amano and Kiel, 2007 for details). **5.** Dorsal view. **8.** view on right valve showing the posterior radial depression; length 16.0 mm.

Distribution: Lower Miocene Honya Formation in Fukushima Prefecture; uppermost lower to lowermost middle Miocene Higashibessho Formation in Toyama Prefecture; middle Miocene Nupinai Formation in Hokkaido (from both seep and whale-fall sites).

Remarks: As shown by Amano et al. (2001), specimens from the Higashibessho locality (Loc. 5) usually have a stouter ventral tooth in the right valve than the specimens from the type locality of "*Vesicomya*" *kawadai* in the Honya Formation. Based on the hinge dentition of the right valve, the presence of a lunular incision and the presence of a small pallial sinus, "*Vesicomya*" *kawadai* is herein transferred to the genus *Pliocardia*.

Comparisons: *Pliocardia kawadai* resembles the Recent species *P. crenulomarginata* (Okutani, Kojima and Iwasaki, 2002) in having a similar hinge dentition in both valves, a radial depressed area from the beak to the postero-ventral corner and a weak ridge before the posterior adductor muscle scar. However, *P. kawadai* differs from *P. crenulomarginata* by having a bifid 3b tooth, no sharply bounded escutcheon and no fine crenulation on the posterior margin.

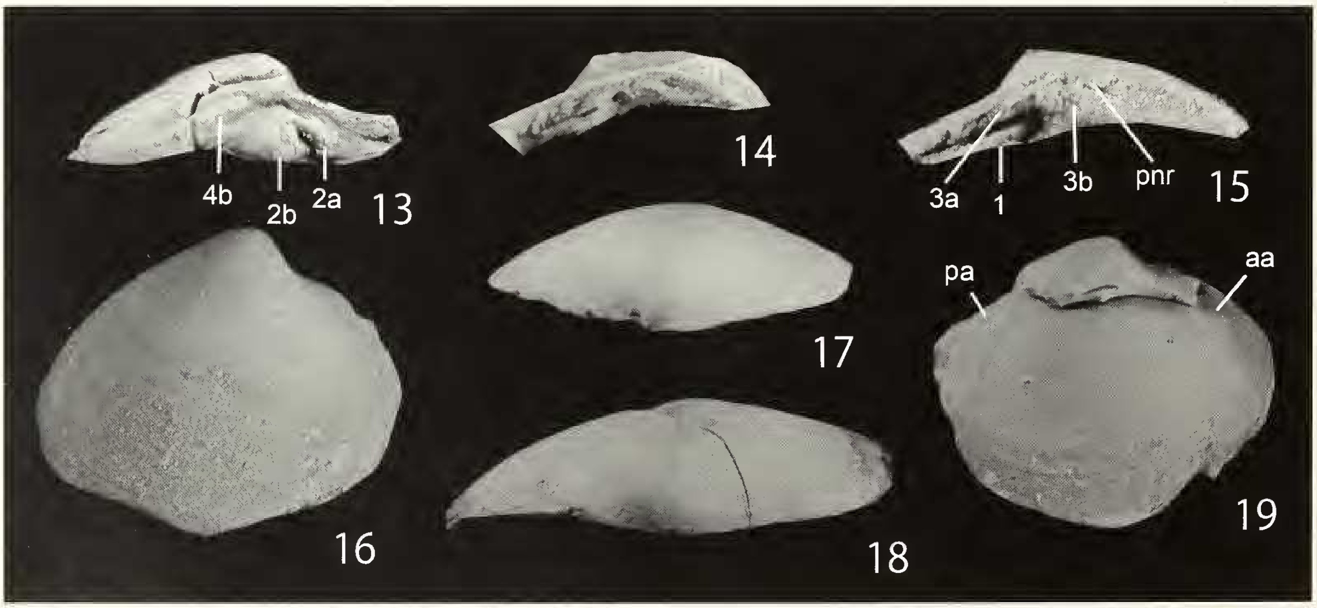
Similar in outline to *P. kawadai* is a species from a seep carbonate in the upper Oligocene part of the Lincoln Creek Formation in western Washington State, USA (Amano and Kiel, 2007). This species is herein only tentatively assigned to *Pliocardia*. We examined additional specimens from this locality (Figures 5, 8) that show a depressed area running from the beak to the posterior corner and a distinct lunular incision. These features, together with the previously described hinge characters (Amano and Kiel, 2007), confirm the assignment of this species to *Pliocardia*, although the presence or absence of a pallial sinus is unknown. This species is much smaller (16.0 mm long) than the up to 40.7 mm long *P. kawadai*.

Genus *Calyptogena* Dall, 1891

Calyptogena veneriformis new species
(Figures 13–19)

Diagnosis: Small-sized *Calyptogena* with veneriform shell, lunular incision lacking, pallial sinus lacking, subumbonal pit lacking. Middle hinge tooth (1) thin, surrounded by U-shaped connection of anterior (3a) and posterior (3b) teeth in right valve, with posterior nymphal ridge.

Description: Shell up to 19.8 mm in length, rather thin, weakly inflated, triangular veneriform (height/length = 0.73–0.88), equivalve, and inequilateral. Antero-dorsal margin concave, continuing to rounded anterior margin; postero-dorsal margin nearly straight into oblique posterior margin at obtuse angle; ventral margin broadly arcuate. Beak prominent, prosogyrate and located at anterior one-third to two-fifth of shell length (i.e., at 29–45% of shell length from anterior margin). Nymph narrow and short. Lunule and lunular incision absent. Escutcheon very narrow, demarcated and deeply depressed. Surface ornamented with growth lines only. Right valve hinge wide for size, with three cardinal teeth, distinct posterior nymphal ridge and subumbonal pit absent. Posterior tooth of right valve (3b) large and triangular; anterior tooth (3a) short and thin, parallel with dorsal margin and connecting with posterior tooth (3b), forming U-shaped connection; middle tooth (1) long and thin, and surrounded by anterior and posterior teeth. Middle cardinal tooth of left valve (2b) stout, connecting with anteriorly oblique anterior tooth (2a); posterior tooth (4b) thin. Pallial line entire. Anterior adductor scar ovate; posterior adductor scar pear-shaped.



Figures 13–19. *Calyptogena veneriformis* new species. All specimens are from the type locality (Loc. 1). **13–15, 18–19.** Paratypes. **13.** Left valve hinge; hinge length 10.0 mm, JUE no. 15899-5. **14.** Right valve hinge; hinge length 6.6 mm, JUE no. 15899-4. **15.** Right valve hinge; hinge length 10.5 mm, JUE no. 15899-3. **18.** Dorsal view of right valve; length 19.1 mm, JUE no. 15899-1. **19.** Inner structure of right valve; length 12.2 mm, JUE no. 15899-2. **16, 17.** Holotype. **16.** Right valve. **17.** Dorsal view of figure 16; length 11.4 mm, JUE no. 15898. pnr, posterior nymphal ridge; aa, anterior adductor scar; pa, posterior adductor scar.

Holotype: Length, 11.4 mm, height, 9.3 mm, JUE no.15898, right valve.

Paratypes: Length, 19.1 mm, height, 15.1 mm, JUE no. 15899-1, right valve; length, 12.2 mm, height, 10.7 mm, JUE no. 15899-2, right valve; length, 6.2 mm, height, 5.1 mm, JUE no. 15899-6, left valve.

Type Locality: Outcrop at Sugawa, Yasuzuka-ku, Joetsu City, Niigata Prefecture (37°03′41″ N, 138°29′22″ E).

Material Examined: Twenty-two specimens from the type locality (Loc. 1 herein).

Remarks: At its type locality *Calyptogena veneriformis* is associated with *Calyptogena pacifica*. A veneriform shell shape is unknown among the Recent specimens of *C. pacifica*, despite the wide range of variation in shell morphology among Recent *Calyptogena* (Krylova and Sahling, 2006; Krylova and Janssen, 2006; Cosel and Olu, 2009). Furthermore, the morphological variation of fossil *C. pacifica* from the Japan Sea borderland shows narrower range than the Recent one (see Kanno et al., 1989; Amano, 2003; Amano and Kanno, 2005; Amano and Jenkins, 2011). We are therefore confident that *Calyptogena veneriformis* represents a new species independent from *C. pacifica*.

Comparisons: Some specimens of *Calyptogena pacifica* have a veneriform shell similar to that of *C. veneriformis* new species (e.g. Krylova and Sahling, 2006, figure 4, H–M). However, *C. veneriformis* can be distinguished from those specimens of *C. pacifica* by its smaller and triangular shell, and its pear-shaped posterior adductor muscle scar. *Calyptogena veneriformis* is also similar to veneriform specimens of *Calyptogena valdiviae* (Thiele and Jaeckel, 1931) from the Gulf of Guinea as illustrated by Cosel and Olu (2009). However, *C. veneriformis* differs from *C. valdiviae* by having a less inflated and triangular shape. Superficially *C. veneriformis* resembles *Wareniconcha guinensis* (Thiele and Jaeckel, 1931) in its veneriform shell. However, *Wareniconcha guinensis* has a narrower hinge plate than *Calyptogena* and a subumbonal pit, unlike *Calyptogena*.

Calyptogena veneriformis resembles some species currently assigned to *Waisiuconcha* Beets, 1942 (e.g., Cosel and Salas, 2001; Krylova and Janssen 2006; Krylova and Sahling, 2010) in having a similar shell form and left valve hinge dentition. But *C. veneriformis* can be distinguished from *Waisiuconcha* by its broad posterior cardinal tooth (3b) and the U-shaped connection between the posterior and anterior cardinal teeth in the right valve, and by the lack of a lunular incision. However, we urge caution about the currently used concept of *Waisiuconcha* because the type species (*W. alberdinae* Beets, 1942) is known from a single left valve only but the taxonomically informative hinge characters among vesicomyids are usually those of the right valve.

Distribution: Type locality only; lower Pliocene part of the Kurokura Formation in Niigata Prefecture, Japan.

Etymology: Named after its veneriform shell morphology.

DISCUSSION

Krylova and Sahling (2010) identified nine living species of *Pliocardia*, which are found in many basins all over the world ocean (Krylova and Sahling 2010). In addition, there are several undescribed or misidentified extant species in museum collections that are also likely to belong to *Pliocardia* (S. Kiel, personal observation). The fossil history of *Pliocardia* is complicated and requires further research. The Miocene *Pliocardia kawadai* is so far the only fossil representative of this genus in Japan. Apart from *P. kawadai* and the late Pliocene type species, the only other fossil species assigned to *Pliocardia* is an as-yet unnamed species from the Oligocene Lincoln Creek Formation in western Washington State, USA (Amano and Kiel, 2007; see also Figures 5, 8). However, several Paleogene taxa from the North Pacific realm that we have previously identified as *Archivesica* (Amano and Kiel, 2007; Kiel and Amano, 2010), as well as "*Vesicomya*" *tschudi* and "*Vesicomya*" *ramondi* from the Oligocene of Peru (Olsson, 1931), show some marked differences to *A. gigas*, the type species of *Archivesica*. They are all considerably smaller than *A. gigas*, many have a lunular incision, unlike *A. gigas*, and some lack a pallial sinus, unlike *A. gigas*. At least some of these Paleogene taxa may belong to *Pliocardia*, or to new genera. This applies also to the oldest known vesicomyid, "*Archivesica*" cf. *tschudi*, from the middle Eocene Humptulips Formation western Washington State, USA (Amano and Kiel, 2007).

If the currently known distribution of fossil *Pliocardia* is taken at face value, it appears that the genus colonized the Atlantic Ocean only very recently, despite its long geologic history. Whereas the genus is known from the northeastern Pacific at least since the Oligocene and from the northwestern Pacific since the early Miocene, the earliest Atlantic record is the late Pliocene type species *P. bowdeniana*. There are several older seep deposits in the Caribbean region, but *Pliocardia* or *Pliocardia*-like shells were reported from none of them (Gill et al., 2005; Kiel and Peckmann, 2007). On the eastern side of the Atlantic Ocean, several Miocene seep deposits are known from Italy, but again, they seem to lack *Pliocardia* (Taviani, 1994; S. Kiel, personal observation). One likely pathway for the colonization of the Atlantic Ocean by *Pliocardia* is the Isthmus of Panama which closed in the early Pliocene about 4.0–3.5 Ma (e.g. Collins, 1996). A passage through this isthmus was recently suggested by Martin and Goffredi (2011) who found that the closest relative (based on molecular evidence) of "*Pliocardia*" *krylovata* from the Pacific side of Costa Rica is the Caribbean species "*Calyptogena*" *ponderosa* Boss, 1968.

Whereas *Calyptogena pacifica* is widely distributed in late Miocene to middle Pleistocene deposits of the Japan Sea borderland (see Amano and Jenkins, 2011), the new species *Calyptogena veneriformis* is only known from lower Pliocene deposit in the central part of the Japan Sea borderland. Thus the geologic age of *Calyptogena veneriformis* coincides with the development of the Omma-Manganji fauna (cf., Otuka, 1939; Amano, 2001, 2007). This fauna is endemic for the semi-enclosed Japan Sea and developed after the separation of the Japan Sea from the Pacific Ocean by uplifting of the backbone mountain range in northeastern Honshu (see Ijima and Tada, 1990). *Calyptogena veneriformis* may thus be considered as part of the Omma-Manganji fauna and may have evolved from *C. pacifica*, the only other species of *Calyptogena* present in this basin during the Pliocene.

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